WATERBIRDS

JOURNAL OF THE WATERBIRD SOCIETY

VOL. 32, NO. 3 2009 PAGES 363-479

Breeding Ecology of Kittlitz's Murrelets at Agattu Island, Aleutian Islands, Alaska

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Abstract.—The Kittlitz's Murrelet (*Brachyramphus brevirostris*) is a poorly-known species of alcid and a seabird of conservation concern. Nesting murrelets were discovered at Agattu Island in the western Aleutian Islands, and a field study provided new information on nest site selection, chick growth rates and reproductive success. Twelve ground nests were located in upland habitats (441 masl) at inland areas of Agattu (2.3 km from shore). All nests contained one egg or chick. Murrelets tended to nest in association with a ground cover of orange crustose lichens, bare ground, small rocks and graminoids. Estimates of growth rates for the body mass of nestling Kittlitz's Murrelets were lower ($K_L < 0.10$) than published estimates for other small-bodied alcids with semiprecocial young ($K_L = 0.14$ to 0.23). Murrelet young departed from nests after 30 days of growth at 47% of adult mass but at 80% of adult wing length. Optimal wing-loading may ensure successful dispersal flights from terrestrial nest sites to ocean habitats. Survival of eggs and young were low during the incubation (0.26; 30 d) and brood-rearing periods (0.22; 30 d), leading to a low probability of nest survival (0.06). Losses during incubation were mainly due to avian predators, whereas mortality of young after hatching was caused by inclement weather. Kittlitz's Murrelets have a suite of life-history traits associated with low reproductive potential (small clutch size, slow growth and poor reproductive success) and may have limited ability to recover from population declines. *Received 27 February 2008, accepted 1 June 2009.*

Key words.—Alcidae, *Brachyramphus brevirostris*, growth rate, nest site selection, reproductive success.

Waterbirds 32(3): 363-373, 2009

Seabirds in the family Alcidae (Order Charadriiformes) are a diverse lineage that includes 13 genera and 23 species found exclusively in north temperate and arctic environments. Life-history strategies of alcids include substantial variation in body size, degree of sociality, nest placement and chick developmental modes (Sealy 1973; Ydenberg 1989; Gaston and Jones 1998). The tribe *Brachyramphini* is a monophyletic lineage of alcids that contains three species: Kittlitz's Murrelets (*Brachyramphus brevirostris*), Marbled Murrelets (*B. marmoratus*) and Long-billed Murrelets (*B. perdix*; Friesen *et al.* 1996a). *Brachyramphus* murrelets are unusual among seabirds because these small-bodied species nest solitarily, on the ground at inland sites and on large tree branches in old growth forests (Murphy *et al.* 1984; Nelson 1997; Day *et al.* 1999; Bradley *et al.* 2004). Nests of murrelets are extremely difficult to locate because these birds use inaccessible sites in remote habitats, because nests are highly dispersed at distances up to 70 km from the ocean, clutch size is only one egg and because the cryptic young are left alone at the nest shortly after hatching. The breeding ecology of Kittlitz's Murrelets remains poorly understood, which is a conservation issue because the global population is small and declining (Kuletz *et al.* 2003; Kissling *et al.* 2007). Possible causes of population declines in Kittlitz's Murrelets include low productivity, changes in food supply caused by glacial recession, disturbance from boat traffic and mortality from gill nets and oil pollution (van Vliet and McAllister 1994; Kuletz *et al.* 2003; Day and Nigro 2004; Agness *et al.* 2008).

The reproductive ecology of murrelets and other seabirds is of particular interest because alcids exhibit great diversity in modes of development and nest departure strategies of the young. In *Brachyramphus* murrelets, auklets (*Aethia*; *Cerorhinca*; *Ptychoramphus*), guillemots (*Cepphus*), and puffins (*Fratercula*), the young are semiprecocial, remain in the nest for 25-50 d and fledge at 40-100% of adult mass. In murres (*Uria*) and Razorbills (*Alca torda*), the young are intermediate in development and leave the nest at about 25% of adult body mass. Finally, in *Synthliboramphus* murrelets, the young are highly precocial, depart the nest within two-four days of hatching at <10% of adult body mass and complete development at sea. After nest departure, semiprecocial young are independent, whereas precocial and intermediate young receive continued provisioning from at least one adult. Thus, *Brachyramphus* murrelets have a unique combination of traits within the family Alcidae and provide an opportunity for researchers to investigate the role of ecological factors in the life-history strategies of an unusual group of seabirds.

Current knowledge of the breeding ecology and nesting distribution of Kittlitz's Murrelets is based on a sample of 24 nests discovered between 1913 and 1994 (Day *et al.* 1983; Day 1995; Day *et al.* 1999; Piatt *et al.* 1999). Most information has been compiled from rare encounters where nests were discovered by flushing incubating adults from eggs. Over 90% of the described nests of Kittlitz's Murrelets have been reported from mainland Alaska and only one nest has been described from the Aleutian Islands (Atka Island; Day *et al.* 1983; Gibson and Byrd 2007). Current population data for Kittlitz's Murrelets is primarily based on coastal surveys of birds in the Gulf of Alaska, where the species is closely associated with tidewater glaciers (Kendall and Agler 1998; Day *et al.* 2003; Kuletz *et al.* 2003; Kissling *et al.* 2007; Agness *et al.* 2008). In the course of a field study of Evermann's Rock Ptarmigan (*Lagopus muta evermanni*; Kaler 2007), we discovered nests of breeding Kittlitz's Murrelets at Agattu Island in the Near Islands group of the western Aleutian Islands. We investigated their reproductive ecology and present new information on nest site selection, breeding phenology and nest survival. Moreover, we calculate the first estimates of growth rates for Kittlitz's Murrelets, and compare our estimates with published rates for other small-bodied alcids with semiprecocial young. Baseline data on the breeding ecology of Kittlitz's Murrelets may provide insights into the proximate causes of ongoing population declines and aid future management efforts for a species of conservation concern.

METHODS

Study Site

Agattu Island (52.43°N; 173.60°W) is part of the Near Islands, a group of five islands in the western edge of the Aleutian Islands and part of the Alaska Maritime National Wildlife Refuge (Fig. 1). Agattu Island is 22,474 ha in area, and most of the land mass is <230 m in elevation. A mountain range composed of seven major submassifs lies along the north side and extends from Armeria Bay eastward to Krugloi Point. The westernmost submassif is composed of five peaks that extend from 518 to 693 m, and include the highest point on the island at 693 m. The dominant plant community is maritime tundra, in part because the climate is consistently cool, wet and windy (Maron *et al.* 2006). During the three-month period from June to August, mean minimum and maximum temperatures were 6.5°C and 9.2°C, total precipitation averaged 6.8 cm per month, and wind velocities averaged 42 kph (climate data from Shemya Island ~30 km northeast of Agattu Island).

Historically, the Aleutian Islands had no native terrestrial mammals west of Umnak Island (Murie 1959;

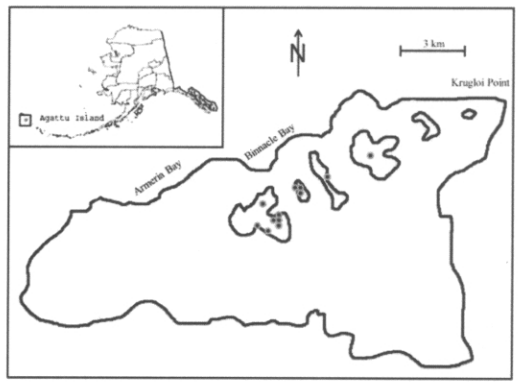


Figure 1. Study location of breeding Kittlitz's Murrelets, Agattu Island, Alaska, 2005-2006. The outline in the northeast portion of the island represents the contour lines of mountainous area at 300 masl. Circles mark locations of twelve nest sites of Kittlitz's Murrelets.

Maron *et al.* 2006; Gibson and Byrd 2007). Many island populations of seabirds and terrestrial birds were impacted by the deliberate introduction of arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*) by Russian fur farmers from the mid-1700s to the late 1800s (Bailey 1993; Ebbert and Byrd 2002; Williams *et al.* 2003). Arctic foxes were successfully eradicated from Agattu by the late 1970s and the main terrestrial predators at Agattu Island include four species of birds. Glaucous-winged Gulls (*Larus glaucescens*) and Common Ravens (*Corvus corax*) are potential predators of eggs and chicks, whereas Peregrine Falcons (*Falco peregrinus*) and Snowy Owls (*Nyctea scandiaca*) may prey upon adult seabirds. Agattu Island does not have an introduced population of rats (*Rattus* spp.) which have negatively impacted bird populations elsewhere in the Aleutian Islands (Major *et al.* 2006).

Field Methods

Murrelet nests were located by intensive ground-searching. We concentrated our search effort in rocky, talus-covered areas along ridges, peaks and terraced slopes at high elevations on major submassifs. Upland habitats ranged from no vegetation to sparse dwarf shrub mats of lichens (*Cladina* spp.), crowberry (*Empetrum nigrum*), heather (*Cassiope* spp.) and other ericaceous plants. Nests were located opportunistically by flushing the incubating adult or by locating unattended chicks. If a nest was located by flushing an incubating bird, we recorded the tail pattern of the adult murrelet. Conspicuous white outer tail feathers are a diagnostic field characteristic of Kittlitz's Murrelets (Day *et al.* 1999). Nest locations were marked with an inconspicuous rock cairn placed ≥10 m from the nest, where we recorded the distance and compass bearing to the nest. Locations of nest sites were measured with a handheld GPS unit (Garmin GPSmap 76; Garmin, Olathe KS, USA) and recorded in Universal Transverse Mercator (UTM) coordinates. Elevation was measured with the GPS unit and later confirmed on a topographic map. Slope angle and aspect were measured to the nearest 10° with a handheld clinometer and compass. In a few cases, multiple nests were located on the same submassif, and straight-line distances between pairs of nest locations were calculated directly from the UTM coordinates.

At first discovery of the nest, we recorded egg length and width (±0.1 mm) and egg mass (±0.5 g), and photographed the nest site. To estimate stage of embryonic development, eggs were floated in a small cup of lukewarm water to determine egg buoyancy. Egg condition was related to stage of incubation as follows: horizontal = 0 d, 45° angle = 5 d, 90° at the bottom of the cup = 13 d, floating at water surface = 16 d and ~ 20 mm diameter circle protruding above the water surface = 20 d (unpublished data).

Nests were visited every four to ten days during incubation, with remote sites receiving less frequent monitoring during the early stages of incubation. To minimize disturbance, we did not flush the attending parent but verified the nest was active by observing the site with binoculars from >30 m. We used egg buoyancy to assess stage of incubation, and then visited nests every three to four days close to the predicted date of hatching to detect newly hatched young. Chicks were visited every three to seven days and we recorded six morphometric traits at each visit. Body mass was recorded on a spring scale (±0.1 g). Flattened wing chord was measured from the carpus to the tip of the longest primary on a wing ruler (±1 mm). Digital calipers were used to take linear measurements of the length of total head and culmen, exposed culmen, tarsus and tail (±1 mm). All measurements were taken between 21.00 and 23.00 h. Nestlings sometimes gave distress calls during handling, and we processed all chicks >30 m from the nest to avoid attracting avian predators to the nest site.

Nest site characteristics were measured immediately after completion of the nesting attempt (Kaler 2007). Vegetation data were collected at each nest site and at four non-use plots placed 50 m from the nest in each of the four cardinal directions. Using a 25-m radius circular plot (0.2 ha) at each nest site and non-use plot, we estimated percent cover for six types of ground cover: bare ground, mesic graminoids, mesic forbs, dwarf ericaceous shrub, dwarf willow shrub and low open shrub (Viereck *et al.* 1992). Using a 5-m radius plot centered around the nest site or non-use plot, we scored percent cover for each of 13 microhabitat features (five types of soil and rock and eight types of vegetation, including orange crustose lichens [*Xanthoria* spp.], bryophytes, graminoids, forbs and shrubs). A single observer recorded all measurements and scored cover on a 10-point scale (0 = <<1%, 1 = <1%, 2 = 1-4%, 3 = 5-10%, 4 = 11-25%, 5 = 26-50%, 6 = 51-75%, 7 = 76-90%, 8 = 91-95%, 9 = 96-100%).

Dates of clutch initiation were calculated by backdating from known hatching dates using a 30 d incubation period (Nelson 1997; Day *et al.* 1999). If an egg hatched between two consecutive visits, the date of hatching was taken as the midway point (accuracy ± 1-2 days). The nest was discovered after hatching in two cases, and we estimated chick age based on their appearance, accumulation of feces at the nest scrape and flight feather growth. The day of hatching was designated as day 1 of the brood-rearing period.

Data Analysis

To determine habitat characteristics associated with Kittlitz's Murrelet nest sites, a stepwise discriminant function analysis (DFA) was used to compare nest plots and non-use plots. Analyses were conducted using Proc Stepdisc and Proc Dscrim of Program SAS (ver. 8.1, SAS Institute, Cary, NC, USA). We calculated median cover scores for each habitat characteristic, and used α-levels of $\alpha \leq 0.5$ for parameter entry and $\alpha \leq 0.2$ for parameter retention in the analysis. We then developed a DFA with the subset of habitat characteristics that were retained in the model, and conducted cross-validation to determine classification rates for nest and non-use plots. The cross-validation procedure classified each plot based on a posteriori probabilities computed across all plots except the plot being evaluated. Aspect of murrelet nests was analysed with circular statistics of Program Oriana (ver. 2.0, Kovach Computing Services, Anglesey, Wales, UK).

Daily survival of eggs and chicks were estimated using the modified Mayfield method (Mayfield 1975; Bart and Robson 1982). Days of exposure were assigned to the incubation or brood-rearing periods from the date of hatching. Dates of failure and fledging were assumed to be the midpoint between consecutive nest checks. Variance of period survival during incubation and brood-rearing and the variance of overall nest survival were estimated using the delta method (Powell 2007).

Growth curves were developed for the six morphometrics recorded for nestling Kittlitz's Murrelets. All growth data were modeled with the logistic function:

$$W = \frac{A}{1 + e^{-K_L(age - I)}}$$

where W is a morphometric trait (e.g. body mass), A is the asymptotic value for that trait, e is the base of the natural logarithm, K_L is the logistic growth rate, *age* is the age of the chick in days, and I is the inflection point when W has reached 50% of A (Starck and Ricklefs 1998). We modeled W as a function of *age* by fixing A and by estimating K_L and I with nonlinear regression and the Marquardt algorithm in Proc Nlin of Program SAS. We initially tested Gompertz and von Bertalanffy growth functions but neither model was a better fit to the growth data than the logistic function (results not shown). To compare growth rates of Kittlitz's Murrelets with other alcids, we fit tangents to the inflection point of the growth curves to estimate the instantaneous maximum growth rates, where $K_LA/4$ is the gains in g per day, and $K_L(N/A)/4$ x 100 is the percent of adult mass gained per day (Sealy 1973; Starck and Ricklefs 1998). We also used the logistic function to calculate the time required for a nestling to grow from 10% to 90% of the asymptotic mass ($t_{10\text{-}90}$).

Estimates of growth rates for alcid young require special care in interpretation due to the wide range of nest departure strategies among species. The growth rate K_L is standardized in relation to asymptotic size, and can be difficult to compare if fledgling young depart from the nest at different developmental stages relative to adult size, or if recession in body mass occurs around the time of fledging. Accordingly, K_L was calculated by setting the asymptotic size in the logistic function to two different values: the maximum size of chicks during brood-rearing, and the final size of adults. Use of adult size controls for continued growth of young after nest departure. We used our field data for maximum size of chicks and took published values for size of adult Kittlitz's Murrelets (Day *et al.* 1999). In all data analyses, we present means ±1SE and considered statistical tests to be significant at $\alpha \leq 0.05$, unless otherwise specified.

RESULTS

Nest Sites and Habitat

Twelve Kittlitz's Murrelet nests were located and monitored at Agattu Island, one in 2005 and eleven in 2006. Nest sites were located on scree and talus-covered mountain slopes (slope = 30° ± 1° SE; range = 10° to 70°; N = 12), at a mean elevation of 441 ± 31 masl (range = 310 to 612 m; N = 12). Straight line distances from nest sites to the ocean averaged 2.3 ± 0.2 km (range = 0.9 to 3.3 km; N = 12). The dimensions of nest scrapes averaged 10.2 ± 0.4 cm in length at the longest axis (range = 8.2 to 13.0 cm) and 3.8 ± 0.3 cm in depth (range = 2.5 to 6.0 cm; N = 12). The mean vegetative cover was 51% ± 5% (range = 30% to 75%; N = 12). Scrapes were typically located on the downhill side of a large rock (>30 cm diameter). Nest sites of murrelets had a random orientation with respect to slope (r = 0.13 ± 0.28; N = 11; Rayleigh test, z = 0.18, P = 0.84). Pairs of Kittlitz's Murrelets were sometimes observed flying near nest sites in upland habitats, and mated birds may have prospected for nest sites together.

Murrelets were not semi-colonial nesters at Agattu Island. Three nests were found on two separate submassifs, and distances among neighboring nests averaged 284 ± 47 m (range = 170 to 356 m) and 419 ± 65 m (range = 29 to 619 m), respectively. In the case where two nests were 29 m apart, the second nest was discovered four days after the first nest was depredated. Egg buoyancy measurements indicated that both nests had been incubated for several days, suggesting that they were attended by different females.

Eleven nest plots were compared with 44 non-use plots in a stepwise discriminant function analysis (DFA). Four of the 19 habitat characteristics were retained as factors that discriminated between nest plots and non-use plots. Retained parameters included cover of orange crustose lichens (partial $r^2 = 0.25$, $F_{1,53} = 16.7$, P = 0.001), bare ground (partial $r^2 = 0.12$, $F_{1,51} = 2.8$, P = 0.014), small rocks (partial $r^2 = 0.07$, $F_{1,50} = 3.9$, P = 0.055), and graminoids (partial $r^2 = 0.04$, $F_{1,52} = 2.0$, P = 0.16). A DFA based on these four factors correctly classified 8 of 11 nest plots (73%) and 32 of 44 non-use plots (73%).

Reproductive Parameters

The breeding period of Kittlitz's Murrelets at Agattu Island ranged from mid-June to late-August. Mean dates of clutch initiation and hatching were 22 Jun (range = 14 Jun to 6 Jul; N = 8) and 22 Jul (range = 14 Jul to 5 Aug; N = 7), respectively. All clutches contained one egg or chick. Eggs were subelliptical in shape and averaged 57.2 ± 0.2 mm in length (range = 54.7 to 60.4 mm), and

38.1 ± 0.2 mm in width (range = 35.0 to 40.9 mm; N = 9). The average mass of fresh eggs (<7 d old) was 46.6 ± 1.1 g (range = 42.0 to 53.0 g; N = 5), or ~21% of adult body mass. Eggs were pale-green with irregular brownish-black, tar-colored spots that ranged from speckling (<1 mm) to broader streaks and patches (<10 mm). Pigmented markings covered the eggs entirely, especially at the blunt end of the egg. During incubation, eggs were always attended by an incubating parent (N = 30 nest visits).

Kittlitz's Murrelet chicks were highly cryptic and their downy plumage resembled a small, gray-brown rock covered with orange crustose lichens. The grayish-brown natal down was interspersed with a speckling of irregular dark spots giving a salt and pepper appearance, similar to rocks and mosses near the nest sites. The front of the head was covered with orange down interspersed with dark spots more distinctly than the rest of the body. Head coloration varied among chicks and ranged in shade from pale yellow to bright orange. Chicks retained the thick layer of natal down during the nestling period until <24 h prior to fledging when they began to remove the down by preening with their bills. Chicks retained the egg tooth during the entire nestling period.

Average chick mass at hatching (<2 d) was 39.2 ± 3.1 g (range = 32.0 to 45.5 g; N = 3), or ~18% of adult body mass. Body mass increased steadily up until day 21 of the nestling period but was more variable prior to fledging at 30 d (Fig. 2). Growth rates of Kittlitz's Murrelets were low whether asymptotic size was fixed as the maximum mass of nestlings at 114 g (K_L = 0.096) or the mass of adults at 224 g (K_L = 0.040, Fig. 2). Maximum growth rates at the inflection point were comparable for both values of asymptotic mass, and were 2.2 to 2.7 g per day or 1.0 to 1.2% of asymptotic mass per day (Table 1). Surviving murrelet chicks fledged at 47% of adult mass at 30 d. Estimates of the duration of the growth period from growth curves based on the asymptotic mass of chicks ($t_{10\text{-}90}$ = 46 d) or adults ($t_{10\text{-}90}$ = 109 d) indicated that development and maturation of young continued at sea after fledging.

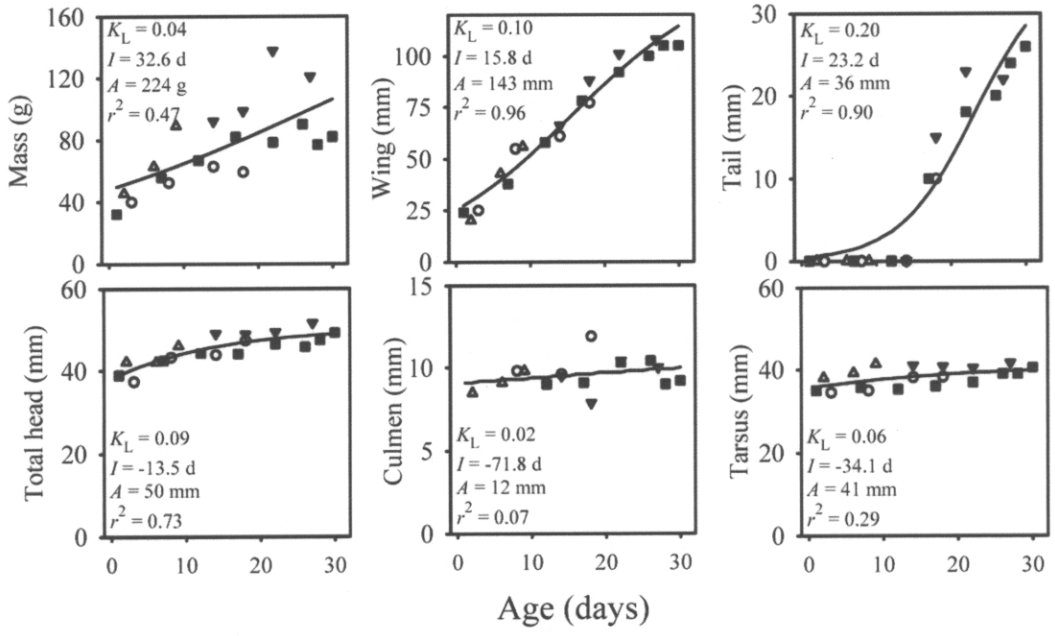


Figure 2. Age-specific growth in six morphometrics of nestling Kittlitz's Murrelets at Agattu Island, Alaska, 2006. Parameters in the logistic growth function include: K_L = logistic growth rate, I = the inflection point (50% of A in logistic growth), A = the asymptotic size of adults (fixed in model), and r^2 = the coefficient of determination. Unique symbols (circles, triangles, squares) represent four known age chicks for which measurements were collected.

Table 1. Growth parameters for the body mass of small-bodied (<300 g) species of Alcidae with semiprecocial young. Growth rates were calculated for Kittlitz's and Marbled Murrelets by setting the asymptotic body size (A_L) to be the maximum mass (g) of nestlings (N) or adult mass (A). Growth parameters include: K_L = the logistic growth rate, $K_LA/4$ and $K_L(N/A)/4 \times 100$ = maximum growth rates of seabird young at the inflection point (in g per d and percent of adult mass gained per d), and $t_{10\text{-}90}$ = the time required for young to grow from 10% to 90% of asymptotic mass (d).

	Mass (g)			Ratios		Growth Parameters					
Species	Nestling (*N*)	Fledgling (*F*)	Adult (*A*)	N/A	F/A	A_L	K_L	$K_LA/4$	$K_L(N/A)/4$	$t_{10\text{-}90}$	Source[a]
Kittlitz's Murrelet	114	102	224	0.51	0.46	N	0.096	2.7	1.2	45.6	1
Brachyramphus brevirostris						A	0.040	2.2	1.0	109.0	
Marbled Murrelet	144	150	221	0.65	0.68	N	0.230	8.3	3.7	19.1	2[b]
Brachyramphus marmoratus						A	0.077	4.3	1.9	56.8	
	166	140	221	0.75	0.63	N	0.144	6.0	2.7	30.5	3[b]
Cassin's Auklet											
Ptychoramphus aleuticus	152	150	167	0.91	0.90	N	0.150	5.7	3.4	29.3	4
Parakeet Auklet											
Aethia psittacula	239	223	297	0.80	0.75	N	0.183	10.9	3.8	24.0	4
Least Auklet											
Aethia pusilla	91	85	86	1.06	0.99	N	0.233	5.3	6.2	—	5[c]
Crested Auklet											
Aethia cristatella	261	239	270	0.96	0.89	N	0.184	11.9	4.4	22.3	4,6

[a]1. This study; 2. Simons (1980); 3. Hirsch *et al.* (1981); 4. Sealy (1973); 5. Major *et al.* (2006); 6. Fraser *et al.* (1999).
[b]Parameters estimated from data in the source manuscript.
[c]Parameters from auklets on islands without introduced rats.

Feather growth started shortly after hatching, and primary and tail feathers began to emerge 5 d and 17 d after hatching, respectively. Wing chord and tail length increased exponentially during the nestling period and reached 50% of adult size at 16 d and 23 d (Fig. 2). At 30 d, murrelets fledged with wings and tails that were 80-81% of asymptotic adult size, respectively. High coefficients of determination ($r^2 \geq 0.9$) indicated that wing chord and tail length would be the best morphometrics for determining age of murrelet nestlings. Total head, culmen and tarsus length showed relatively little change over the nestling period, and negative inflection points ($I < -13$) indicated that most of the growth in the components of structural size occurred during embryonic development (Fig. 2).

Breeding Success

Ten of the murrelet nests were located during the incubation period, and two were found at days 1 and 14 of the nestling period, respectively. Nest fates were determined for eleven of twelve nests; one nest found in 2006 was still active at the end of the season when we left Agattu Island. Daily nest survival for the incubation stage was 0.956 ± 0.019SE (5 losses in 113 d of exposure; N = 10 nests), and the probability of an egg surviving the 30 d incubation period would be 0.26 ± 0.16. Daily nest survival for the nestling stage was 0.951 ± 0.024 (4 losses in 81 d of exposure; N = 6), and the probability of a hatchling surviving the 30 d brood-rearing period would be 0.22 ± 0.17. Overall, nest survival from clutch initiation to fledging, calculated as the product of the two stage-specific rates, would be 0.06 ± 0.03.

The main factor associated with losses during incubation was predation of eggs (80%; N = 5 losses from 10 nests), presumably by Glaucous-winged Gulls, which were more abundant than Common Ravens. The egg in one nest failed to hatch and was abandoned after 38 days of incubation. Eggs in the remaining five nests hatched successfully. During the nestling period, the main cause of losses was inclement weather with three chicks dying from exposure during severe storms and one chick that was depredated at day 8 (75%; N = 4 losses from seven broods). Of the remaining three chicks, one was still alive at our last nest visit on day 9, and two successfully fledged.

DISCUSSION

Little is known about the reproductive biology and distribution of Kittlitz's Murrelets, and new data on nest site selection, growth rates and breeding success are important to understanding the life-history strategies and conservation needs of this elusive seabird. Our discovery of nesting Kittlitz's Murrelets at Agattu Island confirms that this species breeds in the western Aleutian Islands, and our sample of twelve active nests increases the number of known nests by 50% from the 24 nests described in the last century (Day *et al.* 1999; Piatt *et al.* 1999). Discovery of nests was unexpected because seabird surveys in the Near Islands have detected relatively few *Brachyramphus* murrelets near Agattu Island compared with the larger Attu Island (e.g. three vs. 101 birds in July 2003, M. Romano, pers. comm.). Peak counts of murrelets at Attu Island in May to June have ranged from 150-254 birds (Gibson and Byrd 2007). Kittlitz's Murrelets occur at low densities in other areas without glacial ice (Kendall and Agler 1998), but a majority of the estimated global population of 20,000 birds is associated with tidewater glaciers in coastal areas of the Gulf of Alaska (Day *et al.* 2003; Kissling *et al.* 2007; Agness *et al.* 2008). Agattu Island has no glaciers but a remnant glacier remains in the center of Attu Island, presumably from the Wisconsin glaciation period (Gates *et al.* 1971). Habitat associations could differ within the range of Kittlitz's Murrelets in Alaska, and populations from Attu Island in the western Aleutian Islands are genetically differentiated from southcoastal populations at Kachemak Bay (Friesen *et al.* 1996b).

Nest sites of Kittlitz's Murrelets at Agattu Island were dispersed and spatial patterns could reflect the distribution and availability of high elevation upland habitats. Elevation of murrelet nests at Agattu Island (441 m) was intermediate to nests in the northern

(335 m) and southern parts of the breeding range (840 m, Day 1996). Nests ranged from sites with bare soil to vegetative mats of lichens, mosses and ericaceous plants, with an average vegetative cover of 51%. In contrast, most previous descriptions of murrelet nests have reported either no vegetation or vegetative cover of <11%. In two exceptions, nests of Kittlitz's Murrelets found at Tin Creek and Angmakrog Mountain had ground cover values of 25% and 50%, respectively (Thompson *et al.* 1966; Day *et al.* 1983). Our models of habitat selection had moderate success (73%) for classifying nest sites and non-use plots. Orange crustose lichens (*Xanthoria* spp.), and bare ground were the best predictive factors for distinguishing between nest and non-use plots. Similarly, the report of a nest site at Angmakrog Mountain describes crustose lichens and mosses growing among large limestone rocks around the nest depression, and the accompanying illustration of the nest site is dominated by shades of orange (Thompson *et al.* 1966). *Xanthoria* lichens are frequently associated with seabird guano (Wootton 1991) and our observations could indicate reuse of nest sites in different years (Piatt *et al.* 1999). Overall, Kittlitz's Murrelets appear to select nest sites with local microhabitat features that aid in camouflage of the eggs, nestlings and incubating adults.

The average laying date at Agattu Island was 22 June, which was about two weeks later than estimated laying dates for a female collected at Attu Island (8 June 1937, Murie 1959; Gibson and Byrd 2007) and a female collected at Adak Island (9 June 1970, Byrd *et al.* 1974). The female from Attu Island had a post-ovulatory follicle and the egg had probably been laid within the previous few days, whereas the female from Adak Island had a developed egg in her oviduct that would have been laid within a few days. Our average date of hatching was 22 July in the Aleutian Islands, which was comparable to dates compiled by Day (1996) for murrelet nests in mainland Alaska: 3 July 1993 at Kachemak Bay, 22 July 1972 at Frosty Peak, and 27 July 1960 at Angmakrog Mountain.

Interspecific comparisons of K_L among alcids should be made with caution because most estimates have been calculated using mass at fledging as an index of asymptotic size, even though nest departure strategies can vary (Sealy 1973; Ydenberg 1989). Our estimates of K_L and $t_{10\text{-}90}$ from the logistic function were sensitive to whether asymptotic size was set to be nestling or adult mass, but this issue may be less of a problem for estimation of growth in alcids that reach adult size by nest departure. Growth patterns of Kittlitz's Murrelets were typical of alcids with semiprecocial young; nestlings did not reach asymptotic mass by fledging and growth presumably continued after nest departure. However, nestling Kittlitz's Murrelets fledged at only 51% of adult mass, whereas in other small-bodied alcids, including Marbled Murrelets, the young fledge at 65% to 94% of adult body mass (Table 1). Moreover, growth rates based on the asymptotic mass of nestlings were lower in Kittlitz's Murrelets ($K_L < 0.10$) than other small-bodied alcids ($K_L = 0.14$ to 0.23). Using published growth data from Simons (1980), we recalculated K_L for Marbled Murrelets by setting asymptotic size to be the adult mass. Despite nearly identical values for adult mass, growth rates of Kittlitz's Murrelets ($K_L = 0.040$) were 52% of the growth rates of Marbled Murrelets ($K_L = 0.077$), resulting in a developmental period that was almost twice as long ($t_{10\text{-}90} = 109$ d vs. 57 d).

Predation risk and food availability are thought to be two of the most important ecological factors affecting chick development in alcids (Sealy 1973; Ydenberg 1989). In Kittlitz's Murrelets, cryptic nests dispersed at high elevations are likely an adaptation to minimize predation risk. However, a potential cost of nesting in remote habitats could be reduced rates of provisioning that result in slow development of eggs and young, and long periods of exposure. Food resources used by nesting murrelets at Agattu Island were unknown, but low counts on seabird surveys in coastal areas could indicate that birds are foraging long distances from nest sites. Further studies of Kittlitz's Murrelets are needed to determine wheth-

er the growth patterns reported here are a general feature of this species, or are a consequence of nesting on an oceanic island that does not have the preferred foraging habitat of turbid waters associated with glacial outflow (Day *et al.* 2003; Kuletz *et al.* 2003).

Kittlitz's Murrelets fledged at 47% of adult body mass but at 80-81% of adult wing chord and tail length. This combination of traits suggests that wing loading may influence nest departure strategies of Kittlitz's Murrelets. Murrelet chicks fledging with well-developed wings and relatively low body mass may be optimizing wing loading to ensure successful completion of their first flight from the terrestrial nest site to the sea. Departure movements may be long because straight-line distances between nests of Kittlitz's Murrelets and the ocean averaged 2.3 km at Agattu Island (this study), and 15 km for nests at mainland sites (Thompson *et al.* 1966; Murphy *et al.* 1984; Day *et al.* 1999). Similarly, DeSanto and Nelson (1995) reported rapid wing growth of Marbled Murrelets before nest departure, with young fledging at ~86% of the wing length of adults. Alcids with semiprecocial young do not provide parental care after fledging, and wing loading could also be relevant once fledglings have reached the sea where they must learn to evade marine predators and forage by wing-propelled diving.

Despite morphological and behavioral adaptations for concealment and protection, *Brachyramphus* murrelets tend to experience higher rates of nest failure than other alcids (Nelson and Hamer 1995; Gaston and Jones 1998). Our Mayfield estimate of nest survival for Kittlitz's Murrelets was 6%, which was lower than the apparent nest survival of Marbled Murrelets (28%, N = 32 nests, Nelson and Hamer 1995; 48%, N = 116 nests, Bradley *et al.* 2004). Low reproductive success at Agattu Island was due to a combination of egg predation and exposure of chicks to inclement weather. Our field protocols were designed to minimize observer impacts, but some egg losses could have been due to avian predators that were attracted by our activity and located unattended eggs after the incubating parent was flushed. Predation pressure could have been elevated above natural levels at Agattu Island because Glaucous-winged Gulls were locally abundant and sustained by refuse from fish processing facilities in the Aleutian Islands (Gibson and Byrd 2007). Proposed causes of population declines in Kittlitz's Murrelets have primarily focused on events in the marine environment, such as vessel traffic, gill nets and oil pollution (van Vliet and McAllister 1994; Kuletz *et al.* 2003; Agness *et al.* 2008), but our results suggest that factors affecting breeding success in terrestrial habitats could also be important. Poor fledging success among Kittlitz's Murrelets nesting at Agattu Island is consistent with the low productivity reported elsewhere in Alaska (Day and Nigro 2004), and may partly explain why coastal surveys rarely detect hatch-year birds (Kissling *et al.* 2007).

Kittlitz's Murrelets are a rare and declining seabird, and many aspects of their breeding biology remain poorly-known. We have confirmed that Kittlitz's Murrelets are solitary nesters that breed in the western Aleutian Islands. Unexpectedly, murrelets were found nesting in upland habitats of oceanic islands that were a long distance from glacial ice. Reproductive potential was low because of a one-egg clutch size and a long nesting cycle. Despite being a small-bodied alcid with semiprecocial young, Kittlitz's Murrelets had slow rates of growth and fledged at relatively low proportion of adult mass. Understanding the adaptive significance of nest departure strategies of Kittlitz's Murrelets will require further investigation of the proximate causes of egg and chick losses, and the potential tradeoffs between provisioning rates and predation risk to the young and attending parents. Few eggs and chicks survived until fledging and low productivity may be a factor contributing to ongoing population declines. Kittlitz's Murrelets should be managed as a seabird of conservation concern because this species will have limited ability to recover quickly from low population numbers.

ACKNOWLEDGMENTS

Financial support for our work at Agattu Island was provided by the U.S. Missile Defense Agency, the Alaska Maritime National Wildlife Refuge (U.S. Fish and Wildlife Service) and the Division of Biology at Kansas State University. Logistical support for field work was provided by K. D. Bell and the crew of the M/V Tiglax, C. E. Braun, G. V. Byrd, S. E. Ebbert, W. Taylor, G. Wann and the U.S. Coast Guard station at Attu. An anonymous reviewer, G. V. Byrd, J. Fischer, I. J. Stenhouse, J. C. Williams and members of the Avian Ecology Lab at K-State provided statistical advice and reviews of drafts of the manuscript.

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